

THE PROCEEDINGS OF THE HENRY S. DYBAS SYMPOSIUM AT TRI-STATE UNIVERSITY¹

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On November 22, 1980, Henry S. Dybas of the Field Museum of Natural History was awarded an honorary Doctorate of Science from Tri-State University. Henry S. Dybas joined the Field Museum in 1943 and was appointed Curator Emeritus upon his retirement in 1980. Dybas' major research interests are the ecology and evolution of periodical cicadas and the classification and biology of the beetle family Ptiliidae. To commemorate the awarding of the degree, a symposium was held, bringing together several entomologists to discuss research that related to Henry S. Dybas' own work. The moderator was Gene Kritsky of Tri-State University. Abstracts of the papers are presented herein.

An exciting decade with the aquatic Coleoptera.

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New discoveries such as the smallest predaceous water beetle and the first blind, depigmented, aquifer - adapted Dytiscidae can be used to study the tempo of evolution. These water beetles illustrate convergence, and parallel evolution with other beetles. Analogies such as adaptive peaks can be used to symbolize evolution and understand the origin and extinction of species.

The evolution of complex acoustical behavior in cicadas.

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Cicadas and spittlebugs are close relatives that share many characteristics as juveniles and adults. Cicada songs probably evolved from common beginnings with spittlebug courtship sounds, hardly modified in modern Australian *Tettigarctine* cicadas. Cicadas are the only loud insects singing by timballing (which apparently evolved only once), by crepitating (wing-banging, which evolved more than once) and by stridulating (which evolved more than once). These loud species-specific songs are their primary isolating and initial aggregating mechanisms. Male cicadas are the timballing singers — only females of the two species of the Australian *Tettigarcta* have timbals — females of several species also crepitate and stridulate with their

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wings as do their males. Timballing produces the most complex songs; most timbals have either 3 or 4 sound-producing ribs, and many songs show both amplitude- and frequency-modulation. Most cicadas sing only while sitting on vegetation, and only as isolated males. Visual as well as acoustical cues are important in singing, and acoustic directional response has been demonstrated only in females of one species. Some species, however, have evolved group singing by strongly clumped males in "chorus trees" or "chorus bushes," some even synchronizing or alternating individual songs, but a few in Argentina sing only in flight from chorus vegetation with strongly clumped males. Females among many males in these chorusing groups probably measure individual male quality before accepting a mate, but the mechanisms and specific effects of this sexual selection have yet to be identified.

Evidence for a 13-year & 17-year hybridization.

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There are cases where two broods of 17 year cicadas 4 years apart coexist in the same woods. These can be interpreted as being in the process of forming a new 17-year brood that is 4 years accelerated over the previous one. There is some indication that crowding among 17-year nymphs can cause them to delete the 4 year inhibition that normally seems to be programmed as part of their life cycle. If this were to happen repeatedly and be genetically assimilated, it could lead to the evolution of 13-year cicadas from 17-year ones without ever having passed through a life cycle of intermediate length, which would inevitably destroy the periodicity.

There are also cases of two broods of 13-year cicadas coexisting in the same woods. These can not possibly be interpreted in the same way since 13-year cicadas have no 4-year inhibition in growth, and presumably could not grow up in 9 years. An alternative interpretation is that one of the 13-year broods (Brood XXIII) has resulted from hybridization between 13-year Brood XIX and one or another of the 17-year broods. Evidence for this interpretation comes from historical records of a hybridization in 1868 between Brood XIX and Brood X, which resulted in 1898 in the appearance of a new population of Brood XXIII in Dewitt County, Illinois, and the concurrent disappearance of Brood X from that area. A new population of Brood XXIII has also been discovered in Knox County, Illinois, where it appears to have resulted from a hybridization between Brood XIX and Brood III in 1946 and first appeared in 1976.

Theoretically if a 13- and a 17-year brood occur in the same woods, the 13-year brood should readily outcompete the 17-year one. Theoretical reasons are given as to why this should be true.

Competition among cicada species: ecological situations and biological evidence.

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In mature forests the three periodical cicada species show distinct habitat preferences, which serve to keep them separated in space and minimize interspecific competition among them. However, all three species are attracted to the young vigorously growing trees of second growth habitats, where they find themselves stimulated to oviposit in a much wider variety of host species than occur together in mature forests. In second growth, then, interspecies competition does appear to be important, especially since the fungus disease (*Masospora cicadina*) tends to be absent or poorly developed in second growth habitats, and cicadas correspondingly high.

The evidence that competition is important in the population dynamics of a particular cicada species and in the structuring of periodical cicada communities comes from four sources: (1) oviposition preferences of the three cicada species, (2) variable growth rates among nymphs of the same age, (3) mortality of nymphs in crowded populations, and (4) the spatial patterns of nymphs below ground.

A common response of both nymphs and adults to severe competition is to space themselves in ways that reduce its effects. In addition to this the ovipositing adults of each species, when placed in competitive situations, specialize on and increase the use of different diameter categories of twigs for oviposition sites.

The limited mobility of nymphs decreases the probability that they can move away from a severely crowded situation. In those instances, nymphs of 17-year periodical cicadas have three options: (1) abort the usual 4-year inhibition in development, feed faster, and emerge 4 years ahead of schedule, (2) prolong development, feeding longer and emerging in the next year, (3) die in situ. By contrast, 13-year cicada nymphs may utilize the latter two options.

Evolutionary relationships among broods of 13-year and 17-year periodical cicadas.

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This continuing study of the evolution of 13- and 17-year periodical cicadas has used numerical phylogenetic analysis of allozymic and wing-morphometric data to examine the evolutionary relationships of eight broods to date. Initial allozymic studies of three broods of 13-year cicadas

(XIX, XXII, and XXIII) and two broods of 17-year cicadas (XIII and XIV) produced a phylogenetic tree which supported the hypothesis of Lloyd and Dybas; brood formation in the 17-year cicadas preceded brood formation in the 13-year cicadas. Morphometric studies of 48 wing vein characters in these same five broods demonstrated that they could be distinguished from each other via discriminant function analysis. In both allozymic and morphometric analyses broods were well differentiated while populations within broods showed little or no differentiation suggesting that broods are definable evolutionary units.

From considerations of present day biogeography and Pleistocene forest movements, predictions were made as to the relationships of broods appearing in 1978 (Brood I), 1979 (Brood II) and 1980 (Brood III). Both allozymic and morphometric analyses of these broods produced phylogenies in which the 13-year cicadas were monophyletic and most recently derived but the placement of Broods I and II on the allozymic tree supported a "separate Pleistocene refuge" theory of origin while the placement of Broods I and II on the morphometric tree supported the hypothesis of Lloyd and Dybas.